Received: 13 March 2021 | Accepted: 24 June 2021

DOI: 10.1111/jfb.14838

BRIEF COMMUNICATION

JOURNAL OF FISH BIOLOGY fsbi

The use of an unoccupied aerial vehicle to survey shark species over sand and rocky-reef habitats in a marine protected area

Kathryn A. Ayres[1,2] | James T. Ketchum[2,3,4] | Rogelio González-Armas[1] | Felipe Galván-Magaña[1] | Alex Hearn[4,5] | Fernando R. Elorriaga-Verplancken[1] | Edgar M. Hoyos-Padilla[2,4,6] | Stephen M. Kajiura[7]

[1]Instituto Politécnico Nacional, Centro Interdisciplinario de Ciencias Marinas, La Paz, Mexico

[2]Pelagios Kakunjá A.C., La Paz, Mexico

[3]Centro de Investigaciones Biológicas del Noroeste (CIBNOR), La Paz, Mexico

[4]MigraMa, Olema, California, USA

[5]Colegio de Ciencias Biológicas y Ambientales, Universidad San Francisco de Quito, Diego de Robles y Vía Interoceánica, Quito, Ecuador

[6]Fins Attached: Marine Research and Conservation, Colorado Springs, Colorado, USA

[7]Florida Atlantic University, Boca Raton, Florida, USA

Correspondence
Rogelio González-Armas, Instituto Politécnico Nacional, Centro Interdisciplinario de Ciencias Marinas, Av. I.P.N. s/n, Colonia Playa Palo de Santa Rita, Apartado Postal 592, La Paz, Baja California Sur C.P. 23000, México.
Email: rarmas@ipn.mx

Funding information
This study was funded by Pelagios Kakunjá with grants from the Paul Angell Foundation, International Community Foundation, Alianza-Fundación Carlos Slim, Ocean Blue Tree and the National Geographic Society. Student scholarship funding was provided by CONACYT.

ABSTRACT

Cabo Pulmo National Park was established in 1995 and has since seen a large increase in fish biomass. An unoccupied aerial vehicle (UAV) was used to survey shallow coastal habitat in which lemon sharks (*Negaprion brevirostris*), bull sharks (*Carcharhinus leucas*) and Pacific nurse sharks (*Ginglymostoma unami*) were recorded. Sharks were more common in the afternoon, potentially using warmer shallow areas to behaviourally thermoregulate. This study highlights UAV surveying to be a viable tool for species identification, a limitation of previous terrestrial surveys conducted in the area.

KEYWORDS

aerial survey, drone, elasmobranch, monitoring, UAV

Aerial surveying of elasmobranchs has traditionally been completed with manned aircraft, particularly for large species like basking sharks (*Cetorhinus maximus*) (Squire Jr, 1990, Crowe *et al*., 2018) and whale sharks (*Rhincodon typus*) (Gifford *et al*., 2001; Ketchum *et al*., 2013; Rowat *et al*., 2009). Advances in wireless communications and battery technology have led unoccupied aerial vehicles (UAVs), commonly known as "drones," to become integral tools in shark research (Butcher *et al*., 2021). UAVs have either a fixed-wing design, capable of covering large distances, or a multirotor design, capable of covering shorter distances but with the ability to hover (Colefax *et al*., 2018). Multirotor UAVs are particularly applicable for surveying coastal areas where there is contrast between the target species and habitat substrate (Kiszka *et al*., 2016).

For the conservation and management of species populations, it is important that regular abundance surveys are completed (Jachmann, 2001). The potential of UAVs to determine shark abundance has been shown for blacktip reef sharks (*Carcharhinus melanopterus*) in French Polynesia (Kiszka *et al*., 2016), fine-scale movements of small coastal species have been tracked in Australia (Raoult *et al*., 2018) and the shoaling tendencies of *C. melanopterus* (Rieucau *et al*., 2018) and swimming kinematics of blacktip sharks (*Carcharhinus limbatus*) (Porter *et al*., 2020) have also been investigated. UAVs have also captured the attempted predation of *C. limbatus* by great hammerhead sharks (*Sphyrna mokarran*) (Doan & Kajiura, 2020), the predation of a humpback whale (*Megaptera novaeangliae*) by white sharks (*Carcharodon carcharias*) (Dines &

Gennari, 2020), the effects of the presence of whale carcass on shark swimming behaviour (Tucker *et al*., 2021) and multiple species simultaneously feeding (Gallagher *et al*., 2018; Lea *et al*., 2019). In addition, the use of UAVs in the surveillance and detection of potentially dangerous sharks has been explored (Butcher *et al*., 2020; Colefax *et al*., 2020a; Colefax *et al*., 2020b) including identifying optimum light wavelengths to increase detection probability (Colefax *et al*., 2021).

Cabo Pulmo National Park (CPNP) is a small (71 km^2) marine-protected area (MPA) located on the south-east coast of the Baja California Peninsula at the entrance of the Gulf of California, a marginal sea that joins with the Eastern Tropical Pacific Ocean. It was designated as a no-take marine park in 1995, and within 10 years of its creation the fish biomass inside the park had increased by over 400%, including higher trophic-level species (Aburto-Oropeza *et al*., 2011; Bocos *et al*., 2018; Reyes-Bonilla *et al*., 2016). Cabo Pulmo was once a fishing town, but a shift to ecotourism has led to its worldwide recognition for conservation success (Reyes-Bonilla & Alvarez-Filip, 2008). One of the main attractions is the opportunity to scuba-dive with bull sharks (*Carcharhinus leucas*) that have been frequently observed at the park's dive sites since 2011 (Pasos-Acuña *et al*., 2020; Reyes-Bonilla *et al*., 2016). Terrestrial surveys have been carried out since 2013 in a bay called Las Tinajitas (23.4244 °N, −109.43 °W) (Figure 1a,c). On each survey day, observers record sharks from a vantage point in which *C. leucas*, lemon sharks (*Negaprion brevirostris*) and *C. limbatus* are commonly sighted (Asúnsolo-Rivera, 2016; El-Saleh, 2016). The main limitation of these surveys is the accuracy in the identification of species present, even with the additional use of binoculars (El-Saleh, 2016). In this study, the authors trialled the use of a UAV to survey and identify shark species over sand and rocky-reef habitats along the bay.

A small quadcopter DJI Phantom 4 Advanced™ (DJI, Shenzhen, China) was used to complete biweekly (approximately every 2 weeks) aerial surveys between 30 January 2019 and 16 June 2019 at Las Tinajitas. This location was chosen because of the previous terrestrial surveys completed, its accessibility by foot from Cabo Pulmo Town and its location away from frequent dive boat activity that could potentially disturb sharks before surveys. The DJI Go 4 App™ was used to pilot the UAV through a tablet connected to a remote controller with video footage recorded in 4 K high-definition at 30 frames s^{-1}. The UAV was piloted along a 1 km long transect path, within visual-line-of-sight of the pilot, and parallel to the shoreline over shallow (<5 m) sand and rocky-reef habitats (Figure 1a,c). The UAV was flown between 09.00 and 10.00 hours and between 15.00 and 16.00 hours on each sampling day at 4.5 m s^{-1}, with each survey lasting up to 4 min. Surveys were only completed in wind speeds less than 15 knots to ensure that the sea state was relatively calm. The UAV was flown at an altitude of 100 m, which gave a field of view of *c*. 150 m, resulting in the total area surveyed per flight to be 0.15 km^2. During each flight, the camera faced downwards at 90°, and the edge of the shoreline remained within the field of view. If sharks were observed, the UAV was lowered over individuals at an altitude of 10 m to record the species for identification. Environmental factors were taken before each survey flight including time of day (morning/afternoon), tidal height (water level relative to mean lower low water), tidal phase (ebb/flood), cloud cover (on a scale between 0 and 8), wind speed (knots) and sea surface temperature (SST °C). The latter two variables were taken on site with an anemometer and a thermometer, respectively. Water visibility was also recorded using a scale between 1 (excellent) and 5 (poor) depending on how possible it was to view the topography of the seabed. This was determined by the same observer for each flight.

A total of 18 flight surveys were completed, 2 of which were not included in the analysis because of the water visibility being ranked as poor, to minimise availability bias. For all surveys, it was assumed that all sharks present in the transect area were detectable. Video footage was downloaded after returning from the field, and species were identified and counted. Nine of the aerial surveys recorded sharks including *N. brevirostris*, *C. leucas* and Pacific nurse sharks (*Ginglymostoma unami*) (Figure 1b). *N. brevirostris* was identified by the pectoral fins which are distinguishably curved, the origin of the first dorsal fin posterior to the insertion of the pectoral fins and the presence of a second dorsal fin of a similar size to the first (Figure 1e). *C. leucas* was identified by a stout body, rounded head and the first dorsal fin in line between wide pectoral fins (Figure 1d). *G. unami* was identified by a broad head, short rounded pectoral fins, the presence of two dorsal fins of similar size and an elongated caudal fin (Figure 1f).

N. brevirostris was the most common species observed (44% of flights), with individuals either swimming alone or in pairs. On an afternoon survey, two *N. brevirostris* were observed swimming together; the smallest one had a pale colouration and displayed black edges on its pectoral fins, and was likely a neonate (Figure 1g). *C. leucas* were observed on 12.5% of survey flights. On an afternoon survey, five adult *C. leucas* were observed over sand at the most northern point of the transect area, and on another afternoon one adult *C. leucas* was observed swimming over sand (Figure 1d). *G. unami* were observed on 12.5% of survey flights. On one occasion, one adult *G. unami* was observed swimming over both sand and rocks, and on another afternoon survey, eight adult *G. unami* were observed in the north of the transect area, one was first observed swimming over sand before joining seven less-mobile individuals (Figure 1h). *C. limbatus* were not observed in the current study, but were the most common species observed (67% of sightings) on terrestrial surveys in 2013 (Asúnsolo-Rivera, 2016) and have been seen by locals at Las Tinajitas in recent years. Acoustically tagged *C. limbatus* showed a preference for the north of the park (Ketchum *et al*., 2020), and this could explain the absence of recorded sightings in the UAV surveys in the south.

The first record of *N. brevirostris* in CPNP was in 1975, in shallow water close to the shoreline (Reyes-Bonilla *et al*., 2016). The differences in colouration that were observed between *N. brevirostris* are likely because of sun-exposure with larger, older sharks exhibiting darker colourations than younger, smaller sharks, as shown in scalloped hammerhead sharks (*Sphyrna lewini*) (Lowe & Goodman-Lowe, 1996). The presence of neonate *N. brevirostris* could indicate nearby nursery areas, which are yet to be described for this species in the Gulf of California. The first bibliographic record of *C. leucas*

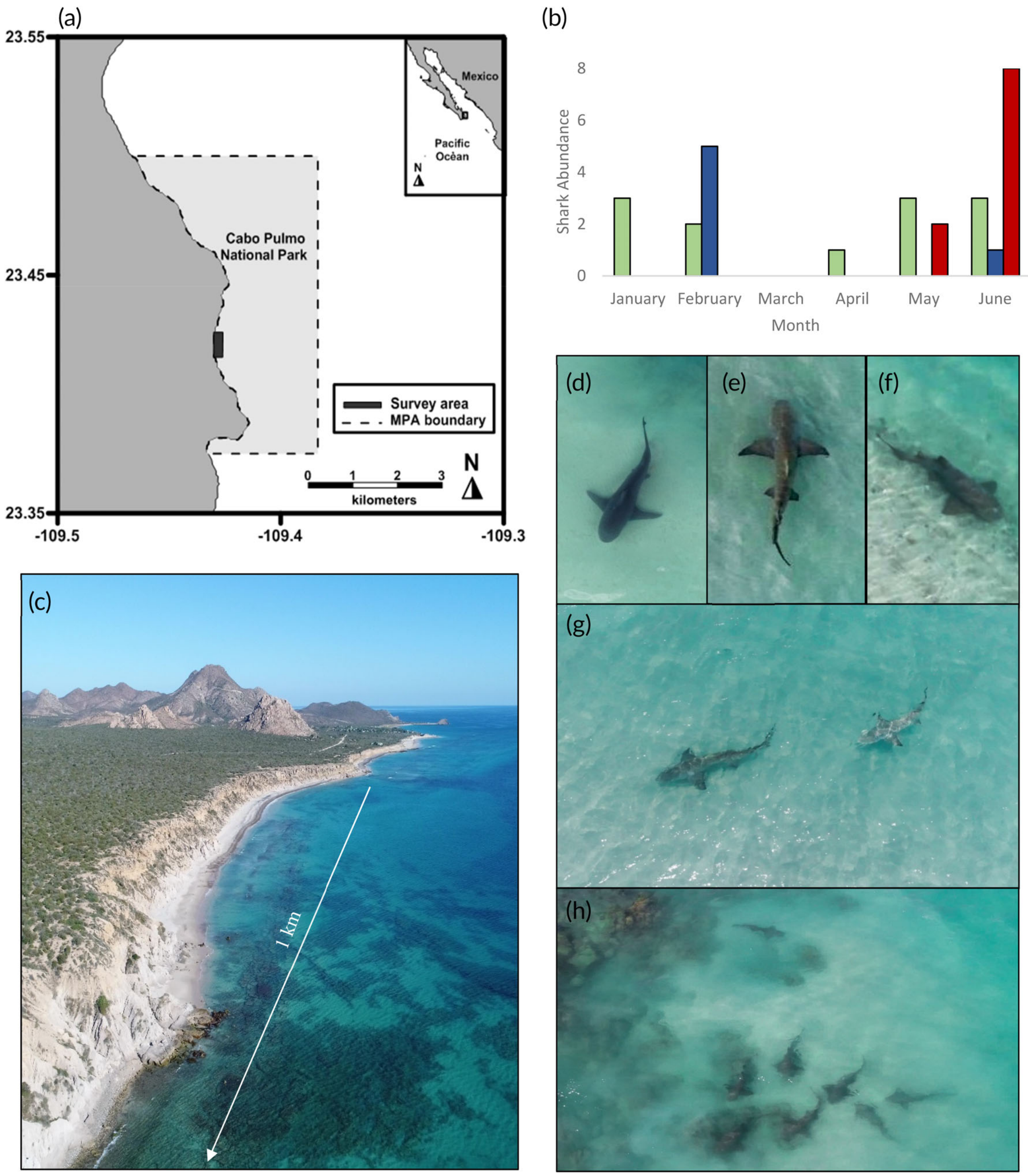

FIGURE 1 (a) Map of Cabo Pulmo National Park and unoccupied aerial vehicle (UAV) aerial survey area. (b) Total shark abundance in transect surveys between January and June 2019 [■ *Negaprion brevirostris*, ■ *Carcharhinus leucas*, ■ *Ginglymostoma unami*]. (c) Survey area with arrow indicating the 1 km theoretical transect path the UAV was flown along. (d) Bull shark (*Carcharhinus leucas*), (e) lemon shark (*Negaprion brevirostris*), (f) Pacific nurse shark (*Ginglymostoma unami*), (g) two *N. brevirostris* displaying different colourations and (h) group of eight *G. unami*

in CPNP was on the main reef in 2011 (Aburto-Oropeza *et al*., 2011). *C. leucas* acoustically tagged in CPNP are monitored by an array of underwater acoustic receivers located along the reef (Ketchum *et al*., 2020). Strong wave action prevents the installation of receivers close to the shoreline; therefore, UAV surveying is an invaluable tool for monitoring this species close to shore. *G. unami* was first observed in CPNP in 2013 and was described as a "rare" occurrence (Reyes-Bonilla *et al*., 2016). *G. unami* is endemic to the Eastern Tropical Pacific and was previously recognised and recorded in CPNP as "*Ginglymostoma cirratum*" which is restricted to the Atlantic and has morphological differences (Moral-Flores *et al*., 2015). It was not recorded in terrestrial surveys in 2013 (Asúnsolo-Rivera, 2016), or in censuses conducted at CPNP between 1986 and 1998 or reported in the literature during this time (Villarreal-Cavazos *et al*., 2000). This species is listed on the IUCN Red List as "Endangered" and so the continued monitoring of the coastline of CPNP will be essential for this endemic species (Pollom *et al*., 2021).

Carcharhinid species can be difficult to distinguish, particularly from aerial surveys when sharks are not near the surface of the water

TABLE 1 Selection of generalised linear model (GLM) using AIC score and deviance explained (%) to predict shark abundance considering the following variables: sea surface temperature (SST °C), wind speed (knots), time of day (morning 09.00–10.00 hours/afternoon 15.00–16.00 hours), tidal height (m), tidal state (ebb/flood) and cloud cover (0–8)

Model	AIC	Deviance explained (%)
Wind Speed + Time of Day + Tidal Height + SST + Tidal State + Cloud Cover	65.37	38.68
Wind Speed + Time of Day + Tidal Height + SST + Tidal State	61.27	36.34
Wind Speed + Time of Day + Tidal Height + SST	63.64	33.35
Wind Speed + Time of Day + Tidal Height**	**63.50**	**29.00**
Wind Speed + Time of Day	66.62	24.02
Tidal Height + Time of Day	65.04	20.70

Note. Model in bold represents final model selected.
**Significant predictor: $P < 0.01$.

(Kelaher *et al*., 2019). In this study, the authors captured footage of sharks in shallow clear water, and surveys with poor visibility were discarded. They are confident that *C. leucas* were identified correctly because of their body and head shape, their proximity to the coastline and owing to the large population present at CPNP. The authors also compared aerial images with underwater photographs of *C. leucas* taken directly above them on SCUBA. *C. limbatus* is also a common carcharhinid in CPNP but can be distinguished from *C. leucas* from an aerial perspective by their long-pointed snouts and more slender body shape. The presence of both *N. brevirostris* and *G. unami* on the UAV surveys was particularly apparent because of their distinctive and recognisable characteristics previously discussed. A guide to the identification of elasmobranch species and other marine fauna from an aerial view, by Colefax *et al*., 2018, can be seen here: https://www.youtube.com/watch?v=nxh2Pp5gq3kf.

Generalised linear models (GLMs) with a Poisson distribution were used to determine which environmental variables were significant predictors of shark abundance. A backwards-stepwise approach determined the final model by subtracting each variable from the full model and assessing the AIC score (Table 1). The final model included four variables: SST, wind speed, tidal height and time of day. Wind speed ranged between 2 and 10 knots across all sampling days and had a slight negative relationship with shark abundance (Pearson's correlation coefficient, $r = -0.10$), SST ranged between 21°C and 26°C and had a slight positive relationship with shark abundance (Pearson's correlation coefficient, $r = 0.14$) and tidal height had a slight positive relationship with shark abundance (Pearson's correlation coefficient, $r = 0.03$). Time of day was the only predictor variable that had a significant influence on shark abundance ($P < 0.01$), with more sharks recorded during afternoon surveys (2.38 ± 2.88, mean ± S.D., $n = 9$) than morning surveys (1.00 ± 1.20, mean ± S.D., $n = 7$). This increase could correspond to an increase in SST over the duration of the day (+ 0.65°C ± 0.26, mean ± S.D.), with sharks moving into the shallow warmer habitat to behaviourally thermoregulate (Economakis & Lobel, 1998, Hight & Lowe, 2007, Speed *et al*., 2012, Thums *et al*., 2013). Continued sampling will determine the extent of the patterns observed between predictor variables (wind speed, SST and tidal height) and shark abundance, as has been shown from the aerial surveying of other elasmobranch species (DiGiacomo *et al*., 2020, Ruiz-García *et al*., 2020, Kaijura and Tellman, 2016).

The main limitation of the study was the inability to survey the area over midday hours because of sun glare. Previous terrestrial censuses found that shark abundance was highest between 13.30 and 14.00 hours (El-Saleh, 2016); therefore, the use of polarised filters and flying with the sun positioned behind the UAV would be recommended for future surveys to reduce glare (Butcher *et al*., 2020). Terrestrial surveys required observers to sit at a vantage point and concentrate for long hours (07.00 to 17.00 hours) in hot conditions, with air temperatures in CPNP reaching over 40°C in summer months. For UAV surveys, the pilot was situated on the beach and could easily seek shade between survey flights. Shark species were difficult to detect and identify from terrestrial surveys, particularly when over rocky-reef because of low contrast, and likely the reason why *G. unami*, a less-mobile species, was not previously observed. Discrepancies between the habitat preferences of *C. melanopterus* at Ninagloo reef were shown between terrestrial surveys and acoustic data. Terrestrial surveys showed that sharks were most common over sandy habitat, whereas acoustic data showed that the reef was more commonly utilised, likely due to sharks being harder to visually detect from land when over reef habitat (Speed *et al*., 2011). In comparison to terrestrial surveys, the UAV flights at CPNP allowed a larger area to be sampled; nonetheless, as a general rule UAVs are required to stay within visual-line-of-sight of the pilot (Butcher *et al*., 2021). Terrestrial surveys in 2013 were also conducted in a second bay further south to Las Tinajitas (Asúnsolo-Rivera, 2016; El-Saleh, 2016); although this bay is within flight range from Las Tinajitas, an additional UAV and pilot would be required to follow visual line-of-sight safety guidelines.

An altitude of 100 m was chosen for the surveys to optimise the total area covered. *C. leucas*, *G. unami* and adult *N. brevirostris* were detected in real-time, which allowed for the pilot to lower the UAV to identify the species. For some surveys, the smaller *N. brevirostris* were only observed post-processing, when footage was reviewed on a larger monitor. Marsh and Sinclair (1989) reported reliable detections from the air at a ratio of 274 m altitude: 1 m length of animal; therefore theoretically, sharks as small as 0.36 m would be detectable from

100 m. In the Bahamas, aerial surveys conducted at 100 m successfully detected *N. brevirostris* of 1 m lengths (Kessel *et al*., 2013). Because of the presence of smaller *N. brevirostris* at CPNP, a lower altitude would be recommended for future surveys. A lower altitude would reduce the width of the survey area but would unlikely affect results dramatically, with the majority of sightings occurring at the wave break. At very low altitudes (<10 m), UAVs have been shown to consistently allow the detection of sharks over a range of habitats, even when not uniform (Hensel *et al*., 2018); nonetheless, the total area covered is compromised because of limitations in UAV battery life. A future experiment involving cut-out replica sharks of varying sizes and colours could establish the most appropriate altitude to be used for surveys in this area (Butcher *et al*., 2020).

Previous assessments of the fish communities at CPNP have been conducted using in-water diving surveys (Aburto-Oropeza *et al*., 2011, Reyes-Bonilla & Alvarez-Filip, 2008, Calderon-Aguilera *et al*., 2021), some of which did not record any sharks, as certain fish species can be deterred by the presence of divers (Watson *et al*., 1995). As surveys using SCUBA are not appropriate for shallow intertidal environments and the inability to install acoustic receivers close to shore, the authors recommend UAV surveying to be included for any future assessments of the ichthyofauna in CPNP, particularly shark species.

ACKNOWLEDGEMENTS

We thank the donors of Pelagios Kakunjá with grants received from the Paul Angell Foundation, International Community Foundation, Alianza WWF-Fundación Carlos Slim, Alianza WWF-Telmex-Telcel, Ocean Blue Tree and the National Geographic Society. Student scholarship funding was provided by CONACYT. The authors thank the Comisión Nacional de Áreas Naturales Protegidas (CONANP) for providing the no objection letter for this research to be completed within the national park (No. PNCP-EXT-0217/2018). The authors also thank M. Grau, H. Sanchez and B. Idalia González Garza for fieldwork assistance and support, and A. Trejo-Ramírez for creating the survey area map. F.G.M., R.G.A. and F.E.V thank Instituto Politécnico Nacional for fellowships (COFAA, EDI). S.M.K. thanks the Colgan Foundation for their continued support.

ORCID

Kathryn A. Ayres https://orcid.org/0000-0003-4646-7004
James T. Ketchum https://orcid.org/0000-0002-7340-4749
Rogelio González-Armas https://orcid.org/0000-0003-4027-6143
Felipe Galván-Magaña https://orcid.org/0000-0002-7613-4617
Alex Hearn https://orcid.org/0000-0002-4986-098X
Fernando R. Elorriaga-Verplancken https://orcid.org/0000-0002-7360-8039
Edgar M. Hoyos-Padilla https://orcid.org/0000-0002-4318-2655
Stephen M. Kajiura https://orcid.org/0000-0003-3009-8419

REFERENCES

Aburto-Oropeza, O., Erisman, B., Galland, G. R., Mascareñas-Osorio, I., Sala, E., & Ezcurra, E. (2011). Large recovery of fish biomass in a no-take marine reserve. *PLoS One*, *6*(8), e23601.

Asúnsolo-Rivera A (2016) Distribución, abundancia y riqueza de especies de tiburones en el arrecife de Pulmo, BSc dissertation, Universidad Autónoma de Baja California Sur, Baja California Sur, Mexico. Available from UABCS library: https://biblio.uabcs.mx/tesis/.

Bocos, A. A., Melo, F. J. F. R., & Bonilla, H. R. (2018). Listado actualizado de peces del arrecife de Cabo Pulmo, Golfo de California, México. *Revista Ciencias Marinas y Costeras*, *10*, 9–29.

Butcher, P. A., Colefax, A. P., Gorkin, R. A., Kajiura, S. M., López, N. A., Mourier, J., … Raoult, V. (2021). The drone revolution of shark science: A review. *Drones*, *5*(1), 8.

Butcher, P. A., Piddocke, T. P., Colefax, A. P., Hoade, B., Peddemors, V. M., Borg, L., & Cullis, B. R. (2020). Beach safety: Can drones provide a platform for sighting sharks? *Wildlife Research*, *46*(8), 701–712.

Calderon-Aguilera, L. E., Reyes-Bonilla, H., Olán-González, M., Castañeda-Rivero, F. R., Perusquía-Ardón, J. C. (2021). Estimated flows and biomass in a no-take coral reef from the eastern tropical Pacific through network analysis. *Ecological Indicators*, *123*, 107359.

Colefax, A. P., Butcher, P. A., & Kelaher, B. P. (2018). The potential for unmanned aerial vehicles (UAVs) to conduct marine fauna surveys in place of manned aircraft. *ICES Journal of Marine Science*, *75*(1), 1–8.

Colefax, A. P., Butcher, P. A., Pagendam, D. E., & Kelaher, B. P. (2020b). Comparing distributions of white, bull, and tiger sharks near and away from the surf break using three tech-based methods. *Ocean & Coastal Management*, *198*, 105366.

Colefax, A. P., Kelaher, B. P., Pagendam, D. E., & Butcher, P. A. (2020a). Assessing white shark (*Carcharodon carcharias*) behavior along coastal beaches for conservation-focused shark mitigation. *Frontiers in Marine Science*, *7*, 268.

Colefax, A. P., Kelaher, B. P., Walsh, A. J., Purcell, C. R., Pagendam, D. E., Cagnazzi, D., & Butcher, P. A. (2021). Identifying optimal wavelengths to maximise the detection rates of marine fauna from aerial surveys. *Biological Conservation*, *257*, 109102.

Crowe, L. M., O'brien, O., Curtis, T. H., Leiter, S. M., Kenney, R. D., Duley, P., & Kraus, S. D. (2018). Characterization of large basking shark *Cetorhinus maximus* aggregations in the western North Atlantic Ocean. *Journal of Fish Biology*, *92*(5), 1371–1384.

DiGiacomo Alexandra, E., Harrison Walker, E., Johnston David, W., & Ridge Justin, T. (2020). Elasmobranch use of nearshore estuarine habitats responds to fine-scale, intra-seasonal environmental variation: observing coastal shark density in a temperate estuary utilizing unoccupied aircraft systems (UAS). *Drones*, *4*(4), 74.

Dines, S., & Gennari, E. (2020). First observations of white sharks (*Carcharodon carcharias*) attacking a live humpback whale (*Megaptera novaeangliae*). *Marine and Freshwater Research*, *71*(9), 1205–1210.

Doan, M. D., & Kajiura, S. M. (2020). Adult blacktip sharks (*Carcharhinus limbatus*) use shallow water as a refuge from great hammerheads (*Sphyrna mokarran*). *Journal of Fish Biology*, *96*, 1–4. https://doi.org/10.1111/jfb.14342.

Economakis, A. E., & Lobel, P. S. (1998). Aggregation behavior of the grey reef shark, Carcharhinus amblyrhynchos, at Johnston Atoll, Central Pacific Ocean. *Environmental Biology of Fishes*, *51*(2), 129–139.

El-Saleh S (2016). The unforeseen recovery of a marine reserve. Abundance, residency and site fidelity of sharks in Cabo Pulmo National Park, Mexico. MSc dissertation, University of Lisboa, Portugal.

Gallagher, A. J., Papastamatiou, Y. P., & Barnett, A. (2018). Apex predatory sharks and crocodiles simultaneously scavenge a whale carcass. *Journal of Ethology*, *36*(2), 205–209.

Gifford, A., Compagno, L. J. V., & Levine, M. (2001). *Aerial surveys of whale sharks (Rhincodon typus) off the east coast of southern Africa from 1993 to 1998*. Princeton, NJ: Report to the Shark Research Institute.

Hensel, E., Wenclawski, S., & Layman, C. A. (2018). Using a small, consumer-grade drone to identify and count marine megafauna in shallow habitats. *Latin American Journal of Aquatic Research*, *46*(5), 1025–1033.

Hight, B. V., & Lowe, C. G. (2007). Elevated body temperatures of adult female leopard sharks, *Triakis semifasciata*, while aggregating in shallow nearshore embayments: Evidence for behavioral thermoregulation? *Journal of Experimental Marine Biology and Ecology*, *352*(1), 114–128.

Jachmann, H. (2001). Introduction to estimating wildlife abundance. In *Estimating abundance of African wildlife* (pp. 3–12). Boston, MA: Springer.

Kajiura Stephen, M., & Tellman Shari, L. (2016). Quantification of massive seasonal aggregations of blacktip sharks (*Carcharhinus limbatus*) in Southeast Florida. *PLoS One*, *11*(3), e0150911.

Kelaher, B. P., Colefax, A. P., Tagliafico, A., Bishop, M. J., Giles, A., & Butcher, P. A. (2019). Assessing variation in assemblages of large marine fauna off ocean beaches using drones. *Marine and Freshwater Research*, *71*(1), 68–77.

Kessel, S. T., Gruber, S. H., Gledhill, K. S., Bond, M. E., & Perkins, R. G. (2013). Aerial survey as a tool to estimate abundance and describe distribution of a carcharhinid species, the lemon shark, negaprion brevirostris. *Journal of Marine Biology*, *2013*, 1–10.

Ketchum, J. T., Galván-Magaña, F., & Klimley, A. P. (2013). Segregation and foraging ecology of whale sharks, *Rhincodon typus*, in the southwestern gulf of California. *Environmental Biology of Fishes*, *96*(6), 779–795.

Ketchum, J. T., Hoyos-Padilla, M., Aldana-Moreno, A., Ayres, K., Galván-Magaña, F., Hearn, A., … Klimley, A. P. (2020). Shark movement patterns in the Mexican Pacific: A conservation and management perspective. *Advances in Marine Biology*, *85*(1), 1–37.

Kiszka, J. J., Mourier, J., Gastrich, K., & Heithaus, M. R. (2016). Using unmanned aerial vehicles (UAVs) to investigate shark and ray densities in a shallow coral lagoon. *Marine Ecology Progress Series*, *560*, 237–242.

Lea, J. S. E., Daly, R., Leon, C., Daly, C. A. K., & Clarke, C. R. (2019). Life after death: Behaviour of multiple shark species scavenging a whale carcass. *Marine and Freshwater Research*, *70*(2), 302–306.

Lowe, C., & Goodman-Lowe, G. (1996). Suntanning in hammerhead sharks. *Nature*, *383*(6602), 677–677.

Marsh, H., & Sinclair, D. F. (1989). Correcting for visibility bias in strip transect aerial surveys of aquatic fauna. *The Journal of Wildlife Management*, *53*, 1017–1024.

Moral-Flores, D., Fernando, L., Ramírez-Antonio, E., Angulo, A., & Pérez-Ponce de León, G. (2015). *Ginglymostoma unami* sp. nov. (Chondrichthyes: Orectolobiformes: Ginglymostomatidae): Una especie nueva de tiburón gata del Pacífico oriental tropical. *Revista Mexicana de Biodiversidad*, *86*(1), 48–58.

Pasos-Acuña, C., Almendarez-Hernández, M. A., Hoyos-Padilla, E. M., Blázquez, M. C., & Ketchum, J. T. (2020). Economic valuation of diving with bull sharks in natural conditions: A recent activity in Cabo Pulmo National Park, gulf of California, Mexico. In *Socio-ecological studies in natural protected areas (pp. 485–509)*. Cham, Switzerland: Springer.

Pollom, R., Avalos, C., Bizzarro, J., Burgos-Vázquez, M. I., Cevallos, A., Espinoza, M., González, A., Herman, K., Mejía-Falla, P. A., Navia, A. F., Pérez Jiménez, J. C., Sosa-Nishizaki, O, & Velez-Zuazo, X (2021). Ginglymostoma unami. The IUCN Red List of Threatened Species 2021: e.T144151831A144151864. https://doi.org/10.2305/IUCN.UK.2021-1.RLTS.T144151831A144151864.en. Downloaded on 09 July 2021.

Porter, M. E., Ruddy, B. T., & Kajiura, S. M. (2020). Volitional swimming kinematics of blacktip sharks, *Carcharhinus limbatus*, in the wild. *Drones*, *4*(4), 78.

Raoult, V., Tosetto, L., & Williamson, J. E. (2018). Drone-based high-resolution tracking of aquatic vertebrates. *Drones*, *2*(4), 37.

Reyes-Bonilla, H., & Alvarez-Filip, L. (2008). Long-term changes in taxonomic distinctness and trophic structure of reef fishes at Cabo Pulmo reef, gulf of California. In *Proceedings of the 11th international coral reef symposium* (pp. 790–794). Fort Lauderdale, FL: Bernhardt RB.

Reyes-Bonilla, H., Ayala-Bocos, A., Melo, F. J. F. R., Zepeta-Vilchis, R., Asúnsolo-Rivera, A., & Ketchum, J. T. (2016). A bibliographic and field record chronology of sharks at Cabo Pulmo National Park, gulf of California. *CICIMAR Oceánides*, *31*(1), 55–57.

Rieucau, G., Kiszka, J. J., Castillo, J. C., Mourier, J., Boswell, K. M., & Heithaus, M. R. (2018). Using unmanned aerial vehicle (UAV) surveys and image analysis in the study of large surface-associated marine species: A case study on reef sharks *Carcharhinus melanopterus* shoaling behaviour. *Journal of Fish Biology*, *93*(1), 119–127.

Rowat, D., Gore, M., Meekan, M. G., Lawler, I. R., & Bradshaw, C. J. (2009). Aerial survey as a tool to estimate whale shark abundance trends. *Journal of Experimental Marine Biology and Ecology*, *368*(1), 1–8.

Ruiz-García, D., Adams, K., Brown, H., & Davis, A. R. (2020). Determining stingray movement patterns in a wave-swept coastal zone using a blimp for continuous aerial video surveillance. *Fishes*, *5*(4), 31.

Speed, C. W., Meekan, M. G., Field, I. C., McMahon, C. R., & Bradshaw, C. J. (2012). Heat-seeking sharks: Support for behavioural thermoregulation in reef sharks. *Marine Ecology Progress Series*, *463*, 231–244.

Speed, C. W., Meekan, M. G., Field, I. C., McMahon, C. R., Stevens, J. D., McGregor, F., … Bradshaw, C. J. (2011). Spatial and temporal movement patterns of a multi-species coastal reef shark aggregation. *Marine Ecology Progress Series*, *429*, 261–275.

Squire, J. L., Jr. (1990). Distribution and apparent abundance of the basking shark, *Cetorhinus maximus*, off the central and southern California coast, 1962-85. *Marine Fisheries Review*, *52*(2), 8–11.

Thums, M., Meekan, M., Stevens, J., Wilson, S., & Polovina, J. (2013). Evidence for behavioural thermoregulation by the world's largest fish. *Journal of the Royal Society Interface*, *10*(78), 20120477.

Tucker, J. P., Colefax, A. P., Santos, I. R., Kelaher, B. P., Pagendam, D. E., & Butcher, P. A. (2021). White shark behaviour altered by stranded whale carcasses: Insights from drones and implications for beach management. *Ocean & Coastal Management*, *200*, 105477.

Villarreal-Cavazos, A., Reyes-Bonilla, H., Bermúdez-Almada, B., & Arizpe-Covarrubias, O. (2000). Los peces del arrecife de Cabo Pulmo, Golfo de California, México: Lista sistemática y aspectos de abundancia y biogeografía. *Revista de Biología Tropical*, *48*(2–3), 413–424.

Watson, R. A., Carlos, G. M., & Samoilys, M. A. (1995). Bias introduced by the non-random movement of fish in visual transect surveys. *Ecological Modelling*, *77*(2–3), 205–214.

How to cite this article: Ayres, K. A., Ketchum, J. T., González-Armas, R., Galván-Magaña, F., Hearn, A., Elorriaga-Verplancken, F. R., Hoyos-Padilla, E. M., & Kajiura, S. M. (2021). The use of an unoccupied aerial vehicle to survey shark species over sand and rocky-reef habitats in a marine protected area. *Journal of Fish Biology*, 1–6. https://doi.org/10.1111/jfb.14838